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Frequency of Twinning in Two Costa Rican Ethnic Groups: An Update

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ABSTRACT Variation in the frequency of twinning among human populations has been presumed to reflect genetic differences. It has been commonly reported that populations of African ancestry have the highest, those of Asian ancestry the lowest, and those of European and Middle-Eastern ancestry intermediate frequencies of twinning. Populations from the Americas have been reported to have intermediate twinning frequencies, presumably reflecting their admixture. In this context, Madrigal (1994. Am J Hum Biol 6:215–218) reported virtually identical (and high) twinning frequencies in two Costa Rican ethnic groups, one of African, the other of Euro-Amerindian ancestry. These frequencies were interpreted in light of frequent inter-ethnic unions, and it was predicted that the two groups would not differ substantially in gene frequencies of several blood enzyme systems. This paper reports the gene frequencies of both groups for such systems. The samples differ significantly for systems that have clearly different frequencies in African and European populations. Given that the groups are actually different in gene frequencies and not homogenous as predicted earlier, the conclusion that twinning frequencies are similar as a result of a similar genetic make up can be questioned. The results challenge the assumption that if populations have similar twinning frequencies it is because they are genetically similar and argue for a stronger environmental component for twinning frequencies. Am. J. Hum. Biol. 13:220–226, 2001. © 2001 Wiley-Liss, Inc.

The study of variation in twinning frequency has been of interest to human biologists and biological anthropologists. Several authors have reported that, whereas East Asian populations have the lowest rate (3–4 per thousand), and Sub-Saharan populations have the highest (at least 16, up to 40–50 per thousand), European and Middle Eastern populations have an intermediate (8 per thousand) frequency of twins in Europe (Bulmer, 1970; Eriksson, 1973; Brues, 1977; Razzaque et al., 1990; Bortolus et al., 1999). In Europe, Spain has been reported to have the lowest frequency of twins (Bulmer, 1970). Population variation in twinning rates appears to be mostly due to dizygotic (DZ) twinning rates (Philippe, 1990), since the monozygotic (MZ) twinning rate is nearly constant at about 3 ½ per thousand (Morton, 1962; Bulmer, 1970).

Population differences in DZ twinning rates have been attributed mainly to genetic variation in gonadotropin production (Khoury and Erickson, 1983), although other factors such as maternal phenotype and various cultural behaviors have also been cited as possible influences (Brues, 1977; Eriksson, 1973; Nylander, 1970; Razzaque et al., 1990). The suggestion of a genetic cause for population differences in twinning rates appeared to be bolstered by reports that admixed New World populations have twinning rates intermediate between those of their parental populations. For example, in the United States, populations of African ancestry have higher frequencies of twinning than do those of European origin, although lower than those reported in Africa (Bulmer, 1970; Eriksson, 1973; Gedda, 1961; Shipley et al., 1967). Specifically in the U.S., "Blacks" have been reported to have a frequency of 12.5 and 13.2, and "Whites" of 10.1 and 10.05 (Bulmer, 1970; Creinin and Keith, 1989; Pollard, 1995).

It was within this framework that Madrigal (1994) investigated the frequency of twinning in two ethnic groups from Limón, Costa Rica. The research setting was ideal to investigate if twinning varies across population lines, since the two ethnic

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groups differed culturally and, presumably, to some extent in their genetic make-up. Afro- Limonenses (AL) are the descendants of a recent migration of Afro-Jamaicans, and Hispanic- Limónenses (HL) are members of the general Costa Rican population, the descendants of Spanish and Amerindian groups. Madrigal's (1994) results were unexpected on several grounds. First, there were remarkably similar twinning rates in both groups (16.75 for AL and 16.86 for HL), both of which were higher than reported in U.S. African- and European-derived groups. The frequencies of the Hispanic group were expected to be lower, given that Spain has the lowest twinning rate in Europe. Since inter-ethnic unions were frequently observed (Madrigal, 1989; Purcell, 1993), Madrigal (1994) proposed that the very similar twinning rates in both groups probably resulted from frequent gene flow between the two groups. That is, although the two groups were discernible culturally, they had exchanged enough genes for a long-enough time so that they would not differ in their genetic make-up, as expressed in the twinning frequency. Madrigal (1994) concluded by mentioning that it would be of interest to determine if the frequencies of serum proteins in both groups indicated that the groups had experienced enough gene flow so that they would not differ in their gene frequencies. The purpose of this paper is to report the results of a serum protein analysis and to update the earlier conclusions.

MATERIALS AND METHODS

Population

Limón is a distinct cultural center in Costa Rica as a result of its Afro-Caribbean population. This group is a product of the immigration in the late 1800s of Jamaican workers to Limón. The laborers were brought to work on the construction of a railroad from the Central Valley to Limón (Bryce-Laporte, 1962; Duncan, 1972; Melendez, 1972; Steward, 1967; Casey, 1979). Having language, religion, and other cultural traits different from those of the remainder of Costa Rica, and having been subjected to racist and discriminatory practices and laws, the Jamaican migrants remained isolated from the general population. Before the 1920s, few Costa Ricans would venture to the Limón area, mostly for fear of the high incidence of malaria. The genetic make-up of the Afro- Limónenses allowed them to survive and succeed in a most difficult tropical ecology, specifically endemic malaria (Madrigal, 1989). Only with increasing in-migration of the larger, Hispanic population beginning in the 1920s did the migrants begin to interact more generally with the rest of the country (Purcell, 1993). The migration of Hispanic Costa Ricans to Limón has increased only in the recent past. According to Purcell (1993), a 1973 estimate of the population in the Limón province indicated that there were 49% White (Hispanic), 46% Black, 3% Amerindian, and 2% Chinese (although Costa Rica does not use ethnic categories in its national statistics). By 1986, however, Blacks were reported to constitute less than 25% of the total population (Purcell, 1993).

With increased migration of Hispanic Costa Ricans to Limón, the proportion of inter-ethnic marriages has also increased. When Purcell (1993) performed his survey of 218 households, 6.5% of all unions were mixed, with 45.2% of respondents approving of such unions. The percentage of inter-ethnic unions, however, is likely to be much higher than that of inter-ethnic marriages. The family structure of Afro- Limonenses has been characterized as having unstable male–female unions and a relatively high proportion of out-of-wedlock births. Thus, while the national average of couples living in common-law unions in 1982 was 4.6%, it was 12.2% in Limón (Chavez et al., 1982). Madrigal also (1989) observed frequent unions between members of the two ethnic groups.

Data

Blood samples and interviews were obtained from a total of 395 individuals. One-half of the data were collected during door-to-door visits, and the other half at the outpatient clinical laboratory service of the Limón Hospital. The subjects attended the laboratory for nongynecological reasons. All subjects denied ever using any method of contraception. The reliability of the data retrospectively reported by the females was tested with intra-class correlations. The data were reliable (Madrigal, 1991). During the interview, the subjects were asked to ethnically/racially classify themselves. The only two terms chosen by the subjects were Black (245 individuals) and White (145 individuals). The blood samples were analyzed for hemoglobin and G-6PD phenotypes at the Investigation Center of Abnormal Hemoglobins and Related Diseases (CIHATA) of the University of Costa Rica [see Madrigal (1989) for laboratory methods]. The samples were also centrifuged and preserved at the Limón hospital and shipped weekly for analysis at the Minneapolis War Memorial Blood Bank in Minneapolis for GCI, Bf, ACP, PGM, and PLG [see Dykes et al. (1983) and Crawford et al. (1984) for the laboratory methods]. Unfortunately, some samples were lost during shipment, so that only 375 are available for genetic analysis.

Gene frequency methodology

The gene frequencies were computed by the gene counting method for each group, and tested for departures from the Hardy–Weinberg equilibrium. For the GCI, BF, and ACP systems In the Afro-Limónense group, there was one observed phenotype whose expectation was less than 0. This resulted in an artificially inflated χ^2 value. In these cases, the phenotype was dropped for the computation of the statistic [see Rickards et al. (1994) and Tartaglia et al. (1995) for a similar situation]. For the G-6PD system, an average frequency was computed from the male and female frequencies. The average frequency was used for computing the expected number of phenotypes in both sexes (according to Hartl, 1988). As suggested by Weir (1996), the hypothesis that the frequencies do not differ between the groups was tested by using a X^2 with Yate's correction for continuity.

RESULTS

Gene frequencies

The gene frequencies of Afro-Limonenses and Hispanic-Limonenses are shown in Table 1. The differences in sample sizes were caused by loss of specimens during shipment. All of the expected phenotypes necessary for Hardy–Weinberg computation are not displayed in the table for brevity. The Afro- Limónense group was at equilibrium for the GCI ($X^2 = 13.95$, d.f. = 15, $P > 0.05$ [Rare Variants = dropped the 1 1 phenotype]), Bf ($X^2 = 2.51$, d.f. = 6, $P > 0.05$ [Rare Variants = dropped the S07 S07 phenotype]), PGM1 ($X^2 = 3.66$, d.f. = 6, $P > 0.05$), ACP ($X^2 = 2.93$, d.f. = 10, $P > 0.05$ [Rare Variants = dropped R R phenotype]), Hb ($X^2 = 11.38$, d.f. = 6, $P > 0.05$), and PLG systems $X^2 = 1.42$, d.f. = 10, $P > 0.05$). The AL group was at disequilibrium for the G6PD system ($X^2 = 88.62$, d.f. = 17, $P < 0.001$ [Rare Variants = collapsed $A^- A^-$, $A^+ B^-$, $B^- B^-$, $A^- B^-$, A^- Var., B^- Var., and Var. Var.]. The Hispanic-Limónense group was at equilibrium for the Bf ($X^2 = 0.663$, d.f. = 6, not significant), PGM1 ($X^2 = 2.80$, d.f. = 6, $P > 0.05$), ACP ($X^2 = 3.56$, d.f. = 3, $P > 0.05$), HB ($X^2 = 0.018$, d.f. = 3, not significant), PLG ($X^2 = 2.84$, d.f. = 6, $P > 0.05$), and G6PD systems ($X^2 = 7.073$ [for both sexes], d.f. = 6, $P > 0.05$ (Rare Variants = collapsed $A^+ A^+$, $A^+ A^-$, and $A^- A^-$ phenotypes). The HL group was at disequilibrium for the GCI system ($X^2 = 15.61$, d.f. = 3, $P < 0.05 > 0.001$). It is of note that in the Afro-Limonense group, the hemoglobin frequencies are close to those expected under equilibrium situations in a malarial environment, with a frequency of Hb A slightly below 90% and a frequency of S and other abnormal hemoglobins slightly over 10%. It is obvious that the Afro-Limónense group is more variable for several systems than is the Hispanic one. Thus, for the GCI, ACP, Hb, PLG, and G6PD systems, the Afro-Limónenses have at least one more allele than do the Hispanics.

The hypothesis that the allele frequencies of these systems do not differ between the groups was tested using a X^2 with Yate's correction for continuity. A system-by-system analysis reveals that the systems for which Africans and Europeans have rather different frequencies are those for which the HL and AL samples differ. Conversely, systems for which African and European populations have similar frequencies are not significantly different between the Limón groups (all European and African frequencies referred to below were taken from Roychoudhury and Nei, 1988). Thus, the Limón groups differed for GCI ($X_c^2 = 49.37$, d.f. = 9, $P < 0.001$), the Afro group having high frequencies of the 1F allele (1F = 0.68) similar in range to those in Africa (0.68 through 0.841 in Sub-Saharan Africa), and the Hispanic group having frequencies of the 1S allele (1S = 0.48), similar to those of French (1S = 0.47), and Basque samples (1S = 0.548). Indeed, when the Limón frequencies were compared to those shown by Crawford et al. (1984), the AL group fell within the African, not the hybrid, and the HL group fell in between the Amerindian and European clusters. The Limón groups

TABLE 1. Gene frequencies of Afro-Limonenses (AL) and Hispanic-Limonenses (HL)

Systems	Phenotypes	AL phenotypic frequencies	HL phenotypic frequencies	Alleles present	Allele frequencies in AL	Allele frequencies in HL
Gcl	1 1	1	0	1	0.01	0
	2 2	2	2	2	0.095	0.188
	1F 1F	49	10	1F	0.68	0.33
	1S 1S	1	24	1A1	0.03	0
	2 1F	8	15	1C10	0.015	0
	2 1S	7	8	1S	0.17	0.482
	1F 1S	23	13			
	1F 1A1	4	0			
	1F 1C10	3	0			
	1S 1A1	2	0			
	Total	100	72			
BF	F F	33	4	F	0.5423	0.219
	F S	56	23	S	0.4197	0.753
	S S	20	42	F1	0.0338	0.021
	F F1	6	1	S07	0.0042	0.007
	F1 F1	0	0			
	F07	0				
	S07 S07	1				
	S F1	2	2			
	S S07	0	1			
	F1 S07	0				
	Total	118	73			
PGMI	1^+ 1^+	92	32	1^+	0.6305	0.527
	1^+ 1^-	49	25	1^-	0.1903	0.232
	1^- 1^-	10	6	2^+	0.1305	0.143
	1^+ 2^+	38	19	2^-	0.0487	0.098
	2^+ 2^+	4	2			
	1^+ 2^-	13	10			
	1^- 2^+	10	7			
	2^- 2^-	0	1			
	1^- 2^-	7	8			
	2^+ 2^-	3	2			
	Total	226	112			
ACP	A A	13	11	A	0.2234	0.281
	A B	67	40	B	0.7697	0.706
	B B	132	60	C	0.0023	0.013
	A C	0	2	R	0.0023	
	B C	1	1	A'	0.0023	
	R R	1	0			
	B A'	1	0			
	Total	215	114			
Hb	A A	185	124	A	0.8797	0.988
	A S	43	2	S	0.1054	0.008
	S S	2	0	C	0.0126	0.004
	A C	4	1	F	0.0023	
	S C	2	0			
	S F	1	0			
	Total	237	127			
PLG	1 1	67	48	1	0.7743	0.783
	1 2	36	20	2	0.2035	0.197
	2 2	5	5	3	0.0089	0.007
	1 B	1	0	B	0.0044	0
	1 D	2	0	D	0.0089	0
	1 E	0	2	E	0	0.013
	1 3	2	1			
	Total	113	76			
G6PD						
Males	A^+	15	1		Average Both Sexes	
	A^-	6	1	A^+	0.16	0.026
	B^+	54	34	A^-	0.055	0.018
	B^-	1	0	B^+	0.74	0.956
	Variant	3	0	B^-	0.02	0
	Total	79	36	Variant	0.025	0
Females	A^+ A^+	12	1			
	A^- A^-	4	0			
	A^+ B^-	1	0			
	B^- B^-	4	0			
	A^+ B^+	12	2			
	A^- B^+	0	1			
	B^+ B^+	115	86			
	A^+ Variant	2				
	B^+ Variant	1				
	Total	151	90			

also differed significantly for the Bf system ($X_c^2 = 35.66$, d.f. = 6, $P < 0.001$), the Afro group having intermediate frequencies of the S allele (S = 0.42), similar to those observed in African groups (ranging from 0.393 through 0.282 in Sub-Saharan Africa) and the Hispanic group having high frequencies of the S allele (S = 0.75), similar to that reported in Spain (S = 0.65). The groups also differed for the Hb system ($X_c^2 = 20.79$, d.f. = 5, $P < 0.001$), with the Afro group having about 12% abnormal hemoglobins, similar to the frequencies observed in Sub-Saharan Africa (close to 10–15%) and the Hispanic group having less than 1% abnormal hemoglobins. Although the frequencies of G6PD (both sexes, $X_c^2 = 21.338$, d.f. = 13, $P > 0.5$) were not significantly different, the corrected X^2 does approach significance, as a result of the very low frequency of the A^+ and A^- alleles in the Hispanic group, similar to the Spain frequencies (the frequency of A^+ and A^- in Spain approaches 0).

The two Limón groups did not differ for PLG ($X_c^2 = 1.83$, d.f. = 6, $0.1 > P > 0.05$), a system for which Europeans and Africans have high frequencies of 1 and intermediate frequencies of 2. The PGM1 frequencies ($X_c^2 = 5.24$, d.f. = 9, $P > 0.05$) did not differ between the groups either, reflecting the similarly high 1+ frequency found in European and African groups. Finally, the Limón groups did not differ for ACP ($X_c^2 = 3.57$, d.f. = 6, $P > 0.05$), reflecting the high B frequency found in Europe and Africa. It should be added that the ACP^{RGUA} variant reported by Barrantes et al. (1982) in Guaymi Costa Rican Indians had a low frequency in the present sample. This probably reflects the fact that the Guaymi have remained relatively isolated from the larger Costa Rican population.

DISCUSSION

The importance of population differences in twinning rate is frequently noted both in the not so recent (Morton, 1962; Bulmer, 1970; Eriksson, 1973; Brues, 1977; Philippe, 1990; Razzaque et al., 1990) and in the more recent literature (Khoury and Erickson, 1983; Hall, 1996; Steegers-Theusnissen et al., 1998; Bortolus et al., 1999). Variation in population-specific levels of gonadotropins is most often cited as the cause (Hall, 1996; Steegers-Theusnissen et al., 1998). Most statements about population differences in the twinning rate have expressed the rates in terms of traditional racial categories; i.e., they have emphasized that "Asians," "Africans," and "Europeans" have significantly different twinning rates while having little heterogeneity within them. It was in this context that Madrigal (1994) reported what were rather unexpected results: two Costa Rican ethnic groups, one of African descent and one of Euro-Amerindian descent, had virtually identical and high twinning frequencies. Given that Madrigal (1989) had witnessed frequent inter-ethnic unions, an observation corroborated by Purcell (1993), it was proposed that the similar twinning rates resulted from similar gene pools brought about by the very frequent gene flow between the groups. Madrigal (1994) concluded that it would be interesting to look at the gene frequencies of these samples, and predicted that the groups would not differ in genetic make-up, since they had virtually identical twinning rates.

This paper reports the gene frequencies, and the results do not support Madrigal's (1994) prediction. The groups differ significantly, or virtually significantly, in every system for which parental African and European populations differ. The gene frequencies suggest that the liberal inter-ethnic unions observed by Madrigal and Purcell were not in place when the subjects were conceived. In other words, inter-ethnic mating does not appear to have been as frequent in the past as it is at present in Limón. Therefore, the suggestion that the two Limón groups had similar twinning frequencies because they did not differ in their genetic make-up must be questioned.

The possibility that the twinning rate might not vary along "racial" lines, as suggested by the literature had been indicated by Pollard (1995, 1996) and more recently by Patel (1997). Pollard (1995) and Patel (1997) found large variations in the frequency of twinning among so-called "Asian" populations in the U.S., and Pollard (1996) found significant differences among different ethnic groups in Malawi. Pollard (1995) concluded that the results suggest that twinning rates are modified by both migration and inter-ethnic mixing. The results of the present study suggest that the environment may play a more important role in the frequency of twinning, and genetic propensity may play a less important role than previously suspected. The subjects appear to be the offspring of mostly within-group mating of two different groups, which had maintained reproductive and genetic isolation. That the two groups had such similar twinning frequencies appears to be best explained as resulting from a common environment, not a common gene pool.

The data analyzed were collected with the intention of having in-depth information about the reproductive history of the subjects, not with the intention of having a large sample of twin pregnancies. Therefore, the small sample size should be acknowledged. However, given that Pollard (1995, 1996) and Patel (1997) had already questioned the homogeneity of twinning frequencies in groups which were supposed to be homogeneous (such as "Asians" and "Africans"), the assumption that twinning significantly differs among large, geographically defined human groups because of genetic reasons can be questioned. The results perhaps indicate the problem associated with dividing humans into the traditional "racial" groups and expecting them to be significantly different for twinning frequencies. Given that it has been well established that most human variation is found within such groups (Lewontin, 1972; Relethford, 1994), researchers should challenge the assumption that these groups are homogenous for the twinning frequency. This is particularly important for New World populations, which have been formed as a result of on-going gene flow among parental populations from Africa, Europe, and the American continent. In conclusion, two ethnic groups from Limón differ significantly for gene frequencies of systems with clearly different frequencies in Africa and Europe. This contrasts with the virtually identical twinning frequency reported previously (Madrigal, 1994). The data suggest that environmental influences may be more important determinants of the frequency of twinning than the supposed genetic, population-based propensity.

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